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Chorus Frogs (*Pseudacris nigrita* LeConte) in South Carolina

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In the southeastern portion of the United States, three species of chorus frogs (*Pseudacris*) have been reported. Two of these species (*P. ornata* Holbrook, *P. brimleyi* Brandt and Walker) are restricted to the coastal plain. The third (*P. nigrita* LeConte) is represented by three subspecies: (1) *P. n. nigrita* in the coastal plain, from North Carolina west to Mississippi; (2) *P. n. verrucosa* Cope on the Florida Peninsula; and (3) *P. n. feriarum* Baird in the piedmont, but extending into the coastal plain on the Gulf coast along the Appalachicola River Valley (Carr and Goin, 1955, p. 184).

In the vicinity of Charleston, South Carolina (Charleston, Berkeley, and Dorchester counties), *P. brimleyi, P. ornata,* and *P. n. nigrita* are common frogs during their winter breeding season. In addition to these frogs, there occurs in this area a fourth form of the genus *Pseudacris,* comparable to *P. n. feriarum* in most features but both larger and more brightly colored in life than *P. n. feriarum* from the South Carolina and Georgia piedmont. Preserved near-topotypic specimens from Pennsylvania are similar to those from the piedmont. The occurrence of these *feriarum*-like frogs well within the known range of *P. n. nigrita* is extremely puzzling and requires a reassessment of the status of the subspecies of *P. nigrita* in the southeast.

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RELATIONSHIPS OF *PSEUDACRIS NIGRITA NIGRITA* AND *PSEUDACRIS NIGRITA FERIARUM*

The case for intergradation between *P. n. nigrita* and *P. n. feriarum* rests upon the work of Neill (1949). Neill regarded as *feriarum* specimens from the South Carolina and Georgia piedmont, a view that has been generally accepted by herpetologists. My own comparisons between southeastern piedmont and the near-topotypic *P. n. feriarum* from Pennsylvania are discussed below in detail. The assignment of frogs from the southeast piedmont to *feriarum* is correct, and differences between the southern and northern populations of *feriarum* are very slight. Neill also points out that intergradation between *feriarum* and *nigrita* occurs in Georgia and South Carolina in the vicinity of the fall line. Specimens from the fall-line area in Georgia, according to Neill, become less *feriarum*-like and more *nigrita*-like as they range progressively farther below the fall line towards the coast. He states that the same intergrading tendencies are present in South Carolina, ranging from true *feriarum* in Edgefield and upper Aiken counties, through intermediates in lower Aiken and Barnwell counties, to true *nigrita* from Allendale County southward.

I have examined 797 specimens of *P. nigrita* from South Carolina, North Carolina, and Georgia. Of these, 179 are *P. n. nigrita* from the coastal plain of these three states, 284 are *P. n. feriarum* from the piedmont and uppermost coastal plain, and 334 are *feriarum*-like individuals from the lower coastal plain in Charleston, Dorchester, and Berkeley counties in South Carolina. Some of these specimens are from areas in which Neill mentions taking intergrades between *feriarum* and *nigrita*. However, none of the material at hand and examined by me shows intergrading tendencies. All specimens from the fall-line area can be assigned without difficulty either to *P. n. nigrita* or to *P. n. feriarum*.

Along the fall line in South Carolina specimens of *P. n. nigrita* have been taken in Kershaw County, while specimens of *P. n. feriarum* have been taken in Aiken, Richland, Sumter, and Kershaw counties. Thus, in Kershaw County, specimens typical of *P. n. nigrita* or *P. n. feriarum* have been collected; no evidence of intergradation between the two forms has been observed in these Kershaw County specimens. In the lower coastal plain, *P. n. nigrita* is known from the following South Carolina counties: Charleston, Berkeley, Dorchester, Colleton, Jasper, Beaufort, Barnwell, and Williamsburg. In the South Carolina piedmont, *P. n. feriarum* is represented by specimens from the following counties: Oconee, Greenville, Pickens, Laurens, Chester, York, Chero-

kee, Fairfield, Greenwood, and Anderson. No *Pseudacris* of any species have been taken within the montane portions of Oconee, Greenville, and Pickens counties. Specimens of *feriarum* from the lower piedmont show no tendency towards *P. n. nigrita,* in either structure or coloration. Likewise, specimens of *nigrita* from the upper coastal plain show no tendency towards *feriarum.*

The calls of *P. n. nigrita* and *P. n. feriarum* are quite distinct. The voice of the former is a slow, ascending scale, the individual crepitations being well separated and resembling the sound made by a finger being drawn across the teeth of a comb. The call of *P. n. feriarum* is faster than that of *nigrita,* the individual crepitations running together into a rather quick ascending scale. Although difficult to characterize verbally, the calls of the two species are so distinct that one can learn to distinguish them aurally without any difficulty. On the night of March 16, 1956, in the company of Richard Thomas and Allan C. Evans (residents of Cheraw, South Carolina), both *P. n. feriarum* and *P. n. nigrita* were heard calling in the immediate vicinity of Cheraw, Chesterfield County, South Carolina, within about 3 miles of each other. Both localities are in the coastal plain, the *feriarum* calling from the flood plain of the Pee Dee River, and the *nigrita* from the flooded ditches and borrow pits in pine woods.

On January 24, 1953, in the company of Julian R. Harrison and John A. Quinby, a large series of *P. n. feriarum* was collected in Kershaw County, South Carolina, at two localities near Boykin. These frogs were taken in roadside ditches after a heavy rain, and they were extremely abundant. On the same evening, a single *P. n. nigrita* was taken 2 miles south of Camden, Kershaw County. It was not calling but was collected as it hopped about on cattails in a flooded ditch that fluctuated in depth along a railroad embankment. In this instance, the specimen of *P. n. nigrita* was taken at a locality closer to the fall line than the specimens of *P. n. feriarum,* which indicates that, at least at this locality, the distribution of these two forms shows a small amount of overlap. That the overlap is greater than is indicated by these records is demonstrated by a lot of four *P. n. feriarum* taken February 26, 1954, 4 miles north, thence 4.8 miles west, of Wedgefield, Sumter County, South Carolina. These specimens of *feriarum* are from a locality farthest removed from the fall line in the upper coastal plain and indicate an overlap of the ranges of the two forms of about 20 miles. These specimens from Kershaw and Sumter counties are readily assignable to *P. n. nigrita* and *P. n. feriarum* and show no evidence of intergradation.

From adjacent states, I have examined specimens of *P. n. nigrita* from the following localities: Georgia: McIntosh, Effingham, and Screven counties (14 specimens); North Carolina: Carteret, Brunswick, Jones, Scotland, and Richmond counties (10 specimens). Twenty specimens of *P. n. feriarum* from Richmond County, Georgia, and five from Orange County and five from Richmond County, North Carolina, make up the balance of specimens studied. None of these shows any evidence of intergradation between *nigrita* and *feriarum*. Especially significant is the fact that the series from 0.75 mile west of Rae's Creek, Richmond County, Georgia, is clearly *feriarum,* with no *nigrita* characters manifested. In North Carolina, both *feriarum* and *nigrita* have been taken in Richmond County, within 5 miles of each other.

From the foregoing discussion, it appears that, at least in South Carolina, *P. n. feriarum* and *P. n. nigrita* behave as though they were full species rather than subspecies. No intergradation has been observed between the two forms in the region of the fall line in South Carolina; rather, the two forms maintain their distinctness in the supposed area of intergradation, and the ranges of the two overlap in this same region. Limited material from North Carolina and Georgia demonstrates the same situation; none of the specimens examined shows any indication of the intergradation described by Neill.

COASTAL PLAIN *FERIARUM*-LIKE SPECIMENS

The occurrence of *P. n. feriarum* within the range of *P. n. nigrita* has been demonstrated by Carr (1940, pp. 56–57) for the Appalachicola flood plain in western Florida. His use of the name *Pseudacris feriarum* in this publication as well as its later use by Carr and Goin (*loc. cit.*) seems well founded on the basis of the evidence in western Florida and South Carolina, for in both of these areas *P. feriarum* and *P. nigrita* occur without intergradation.

As noted above, the occurrence of *feriarum*-like individuals in the South Carolina coastal plain is remarkable. Of the four *Pseudacris* occurring near Charleston, the *feriarum*-like form is most abundant locally and most readily collected. *Pseudacris n. nigrita* (judging from the records of the three winters of 1953–1956) calls from December 15 to May 19 (mid-December to mid-May) in the Charleston area, while the *feriarum*-like frogs call from December 22 to April 17 (mid-December to mid-April). The large choruses of these two frogs occur at distinctly different times: the major *nigrita* choruses extend from about mid-January to late March, while the *feriarum*-like frogs have their peak of breeding activity in late December to mid-January. Thus, by

the time that *P. n. nigrita* choruses are at their peak, the *feriarum*-like frogs are almost finished calling; with only small choruses or scattered individuals persisting until the warm weather of April. The vocalization of these two forms is as distinctive as are the differences noted above between *P. n. nigrita* and *P. n. feriarum*. The call of the *feriarum*-like frogs of the lower coastal plain is more rapid than that of *nigrita*, but is similar to it in that both are ascending scales. Eggs and tadpoles of both forms have been collected, and a study is now in progress comparing these stages in the life history.

The calling sites and breeding situations of *P. n. nigrita* and the *feriarum*-like *Pseudacris* likewise differ. *Pseudacris n. nigrita* calls from flooded pine-wood ditches and borrow pits, gum ponds in pine woods, flooded fields surrounded by pine woods, and in general from wet situations in otherwise xeric habitats. Calling male *P. n. nigrita* are difficult to locate. Males vocalize from the bases of dry herbaceous plants or about dead vegetal debris. In open borrow pits, *P. n. nigrita* invariably is found in the areas where the vegetation is most dense, while *P. ornata*, for example, calls from open, exposed situations at the same localities. Along ditches, *nigrita* calls from the edge of the bank, well concealed by brush and debris. The *feriarum*-like frogs, on the other hand, call from open situations (flooded ditches in mesic woods or open fields with little or no cover), and it is very easy to collect them in large numbers. While calling, the males lie in the open water, supporting the forelimbs on a twig or grass stem, with the legs extended freely behind. In brushy areas, the males are often concealed, but this seems not to be a matter of preference. Open water without vegetation is used more often by the *feriarum*-like frogs than by *nigrita*.

The relative strength of choruses of these two frogs is strikingly different. On only one occasion has a chorus of *P. n. nigrita* been heard which approached the usual large choruses of the *feriarum*-like chorus frogs. Along the road between Charleston and Summerville (South Carolina Route 61) choruses of *feriarum*-like *Pseudacris* are common during the height of the breeding season, and the woods resound with the harsh calling of this form. It is thus remarkable that these *feriarum*-like frogs have not been previously recorded from the Charleston region, and, especially so, in consideration of the fact that Charleston and its vicinity were the source of many early herpetological specimens on which original descriptions were based.

The range of the *feriarum*-like form in the lower coastal plain is apparently restricted to Charleston, Berkeley, and Dorchester counties (see fig. 1). Marginal known localities of occurrence, beginning at

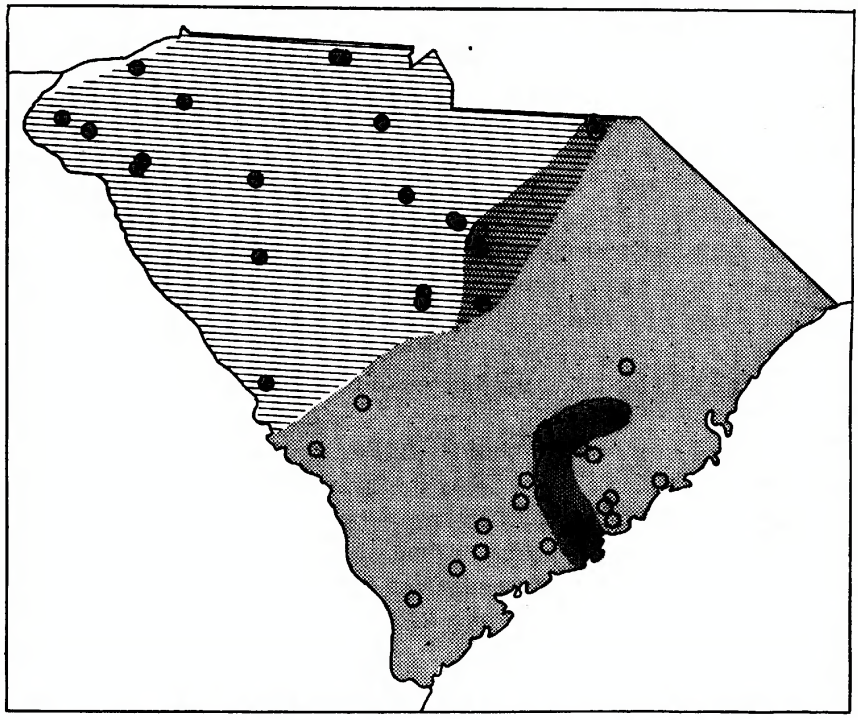

FIG. 1. South Carolina, showing the distribution of the three forms of *Pseudacris* of the *nigrita* group. Horizontal lines and solid circles, *P. n. feriarum;* stippling and hollow circles, *P. n. nigrita;* vertical lines and half-solid circles, *feriarum*-like individuals in the coastal plain. Overlap of symbols represents overlap of range, not intergradation of forms represented.

Charleston and going clockwise, are: 4 miles west of Charleston, 8.4 miles southeast of Holly Hill, 1 mile north of Monck's Corner, and Alvin. Along the coast, there are no records east of the Cooper River or from the area between the Cooper and Santee rivers, despite much mid-winter collecting in this area, as well as to the southwest along the coast. The reason for this restricted distribution is unknown. To the north and east of Charleston, extensive stands of pine woods apparently offer a habitat that is unsuitable for these *feriarum*-like frogs. Both *P. ornata* and *P. n. nigrita* are the characteristic chorus frogs of this pine-woods area. To the southwest and west of Charleston, the country is essentially similar to that inhabited by the *feriarum*-like frogs, but such deciduous woods are regularly inhabited by *P. brimleyi,* with scattered choruses of *P. n. nigrita* and *P. ornata* in locally suitable areas.

In one instance, calling *P. n. nigrita* and *feriarum*-like frogs have been taken calling in the same locality; this was a flooded grassy field, 7 miles northwest of Charleston. This locality is typical breeding habitat for the *feriarum*-like frogs and not for *P. n. nigrita.* The habitat preferences of the two forms are remarkably effective. Often choruses of both frogs may be heard in the same immediate area, but only rarely at the same pond. In wooded areas, the *feriarum*-like frogs are most often associated with *P. brimleyi,* although the latter calls from more secretive stations than does the former. *Pseudacris n. nigrita* and *P. ornata* are usually associated at calling localities.

That this preference for calling habitat is effective in maintaining the distinct characters of the two forms is demonstrated by the fact that, of 334 *feriarum*-like individuals examined from the coastal plain, none shows any tendency towards *P. n. nigrita,* and likewise all the lower coastal plain *P. n. nigrita* are definitely that form and show no approach to the characters of the *feriarum*-like individuals.

The *feriarum*-like frogs of the lower coastal plain are separated from the piedmont *P. n. feriarum* by approximately 60 miles of area that appears, at the present writing, to be uninhabited by any *P. n. feriarum* or *feriarum*-like *Pseudacris.* The locality nearest to the coast from which *P. n. feriarum* has been taken is 4 miles north, thence 4.8 miles west, of Wedgefield, Sumter County, while the farthest inland record for the *feriarum*-like frogs is Alvin, Berkeley County. There is of course the possibility that the lower coastal plain populations are confluent with the piedmont and upper coastal plain populations in this intervening area. However, no material is available to demonstrate that such is the case.

COMPARISONS

Inspection of table 1 reveals the following facts. Comparison of series of males from the South Carolina piedmont with males from near the type locality of *P. n. feriarum* shows that, for the five measurements taken, the averages between these two series are remarkably similar. Females, of which less adequate material is available for comparison, average somewhat larger in all measurements in the piedmont. On the basis of measurements, it seems apparent that the southern piedmont material is correctly assigned to *P. n. feriarum.* Comparison of the measurements of two series of *feriarum*-like individuals from two localities in the South Carolina coastal plain gives some indication of the amount of variation in size within the coastal plain, *feriarum*-like populations. The series of 15 males from Charleston

TABLE 1

MEASUREMENTS (MEANS AND OBSERVED RANGES) IN MILLIMETERS OF FOUR SAMPLES OF *Pseudacris nigrita* FROM FOUR GEOGRAPHIC AREAS

(The Pennsylvania data are based on near-topotypes of *P. n. feriarum*, while the piedmont material from South Carolina is from Cherokee County.)

Locality	Sex	No.	Snout–Vent	Head Width	Head Length	Tibia	Fourth Toe
Pennsylvania	♂	33	24.1(19.8–27.3)	8.5(7.0–10.0)	7.3(6.2–8.6)	12.1(9.8–14.0)	11.1(9.2–12.5)
South Carolina piedmont	♂	33	24.3(21.3–28.5)	8.6(7.3–10.2)	7.4(5.7–8.5)	12.2(9.0–14.7)	11.1(9.8–13.4)
Charleston Co.; S.C. coastal plain	♂	15	33.0(31.4–34.6)	11.2(10.0–11.9)	9.6(9.0–10.9)	16.0(13.8–17.5)	14.5(13.4–15.6)
Dorchester Co.; S.C. coastal plain	♂	18	27.3(25.0–30.5)	9.9(9.0–11.3)	8.5(7.5–9.4)	13.9(12.7–14.7)	12.2(11.0–13.5)
Pennsylvania	♀	6	25.1(22.5–27.2)	8.5(7.6–9.0)	7.4(6.9–7.9)	12.8(11.8–13.3)	11.5(10.4–12.1)
South Carolina piedmont	♀	7	27.3(22.4–30.8)	8.9(7.5–10.7)	8.2(6.8–9.7)	13.6(11.0–16.0)	12.2(9.0–14.8)
Charleston Co.; S.C. coastal plain	♀	3	37.9(36.6–38.5)	11.9(11.7–12.1)	10.1(10.0–10.2)	18.3(18.2–18.5)	15.9(14.8–16.8)
Dorchester Co.; S.C. coastal plain	♀	2	34.7(33.2–36.1)	11.3(11.0–11.6)	10.1(9.7–10.5)	16.6(16.5–16.7)	15.5(14.7–16.3)

County averages larger, in all measurements taken, than a series of 18 males from Dorchester County. Females show about the same situation, although, probably because of the smaller number measured, the differences are not so great as are demonstrable between the males from the same localities.

When coastal plain males are compared as a unit with piedmont males, the average larger size of the former is at once apparent. This size difference is so great that specimens in the hand are readily assigned to one area or the other in most cases, merely on the basis of over-all size. There is an overlap between the smallest measurements of coastal plain frogs and the largest measurements of piedmont males. In females, this difference is even more striking, as there is almost no overlap between measurements, the coastal plain females being much larger than the piedmont frogs.

Smith and Smith (1952) discuss the relationships and means of differentiation between the subspecies *P. n. feriarum* and *P. n. triseriata.* They find that in *P. n. feriarum,* the ratio of tibia length to snout–vent length is usually 47 per cent or higher, averaging 50.6 per cent in the specimens they examined. Comparison of the data from the present study with those of Smith and Smith indicates that these authors are correct. Of the near-topotypic *feriarum* from Pennsylvania, only one individual has a tibia/snout–vent ratio lower than 47 per cent; and of the *feriarum*-like individuals from the Charleston area, five are below 47 per cent in the tibia/snout–vent ratio. Means and observed ranges of this ratio for these three series are: Pennsylvania, 50.3 (43.1–54.4); South Carolina piedmont, 50.5 (45.0–56.8); Charleston area, 49.7 (42.3–52.9). The close similarity between Smith and Smith's average of 50.6 per cent for *P. n. feriarum* and the Pennsylvania and South Carolina piedmont specimens is evident. The material from the South Carolina coastal plain appears to have a slightly shorter tibia, when compared with piedmont and Pennsylvania *P. n. feriarum,* but the difference is not statistically significant.

Smith and Smith (1952, p. 167) define *P. n. feriarum* as: "A subspecies of *P. nigrita* with a dorsal pattern varying from distinct longitudinal stripes to speckled or even plain; most often dorsal stripes either much interrupted or very narrow and not extending from orbital region all the way to the vent; lateral stripes nearly always prominent, often accentuating weakness of dorsal pattern; ground color fawn, gray, tan, or even pink with stripes or flecks of brown, black, or olive; venter cream colored, usually with dark stippling on breast; upper parts of limbs lightly speckled, dashed, or plain; upper jaw with

a light stripe, narrowly margined below with dark; triangle usually present between eyes." This description agrees generally and in detail with the material from Pennsylvania, and the piedmont and coastal plain of South Carolina. Comparison of the ventral color of specimens from the piedmont and coastal plain of South Carolina shows that those from the coastal plain regularly have brighter yellow venters. The ventral color of a series of 11 *P. n. feriarum* from Anderson County, South Carolina, varies between Marguerite Yellow and Reed Yellow (all capitalized color names from Ridgway, 1912), while a series of three specimens from the Charleston region has the ventral coloration varying between Apricot Yellow and Deep Colonial Buff. The brighter and deeper yellow coloration of the coastal plain material is at once evident.

There is a strong tendency for the *feriarum*-like specimens from the vicinity of Charleston to lack an interocular bar or triangle. Of 60 specimens examined from this area, eight have the bar well defined, 17 have it poorly defined, and 35 lack the bar entirely, the interocular space being either plain or variously mottled with dark dots or blotches. The series of 39 specimens from Pennsylvania shows the following proportions: bar well defined, 21; bar poorly defined, 11; bar absent, seven. Sixty-eight specimens from the South Carolina piedmont show: bar well defined, 35; bar poorly defined, 21; bar absent, 12. A chi-square test of these data demonstrates that the observed and theoretical frequencies differ most strongly in the coastal plain specimens, there being fewer specimens with well-defined bars and more with the bar absent than are theoretically probable.

The taxonomic status of the *feriarum*-like individuals from the South Carolina coastal plain is unknown. The local situation appears to resemble in some ways the occurrence of *P. n. nigrita* and *P. n. feriarum* (or *P. feriarum*) in western Florida. The absence of demonstrable intergrades between the coastal plain (*nigrita*) and the piedmont (*feriarum*) populations in South Carolina, and the geographic overlap of the ranges of these two forms along the fall line, are certainly indicative of a specific, rather than subspecific, relationship. Likewise, the occurrence of *feriarum*-like populations in the coastal plain of South Carolina, well within the range of *P. n. nigrita* and not intergrading with this form, apparently disjunct from the "parent" piedmont *P. n. feriarum* populations, and with breeding time and preferred sites different from *P. n. nigrita,* tend also to show that *P. nigrita* and *P. feriarum* might better be regarded as full species. Apparently

the sole published evidence for intergradation between *P. n. feriarum* and *P. n. nigrita* rests on the work of Neill (1949).

The collection of additional specimens from intermediate areas in the southeast and elsewhere from regions where intergradation between *P. nigrita* and *P. feriarum* might be expected, as well as studies currently in progress by Charles F. Walker, may reveal that these two forms intergrade (or hybridize?) locally. In our present state of knowledge concerning the chorus frogs of the eastern United States, it seems preferable to regard *Pseudacris nigrita* as distinct from *Pseudacris feriarum*. Smith and Smith (1952) have shown that *P. n. feriarum* (= *P. feriarum* as used in the present paper) intergrades with *P. n. triseriata* in the central Mississippi region. *Pseudacris n. maculata* has been shown to intergrade with *P. n. triseriata* (Smith, 1956) also. Harper (1955, p. 4) likewise intimated intergradation between *P. n. kalmi* and *feriarum* in northern New Jersey and the piedmont of Pennsylvania. On the basis of these facts, the subspecies currently referred to *P. nigrita* should be rearranged as follows:

Pseudacris nigrita nigrita LeConte, 1825
Pseudacris nigrita verrucosa Cope, 1877
Pseudacris triseriata triseriata Wied, 1839
Pseudacris triseriata maculata Agassiz, 1850
Pseudacris triseriata feriarum Baird, 1854
Pseudacris triseriata kalmi Harper, 1955

The occurrence of *feriarum*-like individuals near Charleston lends strong support to the separation of *P. nigrita* and *P. feriarum* as species. The sympatric occurrence of two races of a single species in a given geographic area is not unknown, yet in the present instance there is little reason for our assuming that such is the case. All the evidence from the present study points to the probability that *P. nigrita* and *P. feriarum* are distinct species. Thus the coastal plain population of *feriarum*-like frogs appears to be a local population, derived from *feriarum* on the piedmont, and only remotely (not subspecifically) related to *P. n. nigrita* with which it occurs.

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lent me a small collection of *Pseudacris* from North Carolina for study, and Mr. Neil D. Richmond (Carnegie Museum) has allowed me to examine a series of *P. n. feriarum* from Pennsylvania.

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